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A study of community structure and beta diversity of epiphyllous liverwort assemblages in Sabah, Malaysian Borneo

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Abstract

We evaluated the species richness and beta diversity of epiphyllous assemblages from three selected localities in Sabah, i.e. Mt. Silam in Sapagaya Forest Reserve, and Ulu Senagang and Mt. Alab in Crocker Range Park. A total of 98 species were found and a phytosociological survey was carried out based on the three study areas. A detailed statistical analysis including standard correlation and regression analyses, ordination of species and leaves using centered principal component analysis, and the SDR simplex method to evaluate the beta diversity, was conducted. Beta diversity is very high in the epiphyllous liverwort assemblages in Sabah, with species replacement as the major component of pattern formation and less pronounced richness difference. The community analysis of the epiphyllous communities in Sabah makes possible their detailed description and comparison with similar communities of other continents.

Keywords

Lejeuneaceae, liverworts, Malesia, Marchantiophyta, statistical analyses

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Introduction

Beta-diversity can be defined as the change or turnover in species composition among particular sites (Anderson et al. 2011). This pattern provides a platform into understanding processes that form and maintain biodiversity (e.g., Tuomisto et al. 2003; Chase 2010; Anderson et al. 2011; Kraft et al. 2011). According to Whittaker (1972), the level of beta-diversity in plant communities is associated with two mechanisms known as habitat heterogeneity and dispersal limitation. This has brought the attention of ecologists to further assess the patterns of beta-diversity and to investigate the mechanisms behind observed patterns through specifically designed data collection (Smith 1982; Bolnick et al. 2002; Harrison et al. 2006; Philippot and Hallin 2011; Myers et al. 2013). Hence, epiphyllous liverworts communities seem to give advantages and provide an excellent system for the study of beta diversity (Kraichak 2014) in numerous ways. First, they can be easily sampled and obtained in a large number within a relatively small area and extended across multiple habitat types and scales (Kraichak 2014). They usually occur and thrive well in moist and warm forests of tropical and subtropical regions (Chen and Wu 1964) and can be preserved intact for later examination (Richards 1932). Besides, due to their simple morphological structure and poikilohydric status, they rely greatly on air moisture as the condition of survival, allowing reliable quantification of particular resource levels and fluctuations (Monge-Najera 1989; Pócs 1996; Gradstein 1997; Pócs and Tóthmérész 1997; Zotz et al. 1997).

Liverworts commonly occur as epiphytes and epiphylls in tropical rainforests (Gradstein 1997; Gehrig-Downie et al. 2013). The epiphylls or epiphyllous liverworts (i.e. species found growing on the living leaves of vascular plants) constitute a special life form, occurring in permanently moist and warm evergreen forests in tropical and subtropical regions. They are considered as the most important component in epiphyllous assemblages, in which an average of 4–8, but sometimes much more, up to 25 species, can grow on a single leaf (Lücking 1995; Gehrig-Downie et al. 2013). In addition, they often exhibit high rates of endemism, especially in montane forests above 1,500 m elevation (Pócs 1996). Epiphyllous liverworts have been described since the 18th century; the first report of an epiphyllous liverwort, i.e., *Jungermannia flava* Sw. (= *Lejeunea flava* (Sw.) Nees), was given by Swartz in 1788. Since then, epiphyllous liverworts have attracted and captured the interest of numerous botanists and ecologists because of their unique habitat, their life strategies, and adaptations necessary for surviving in such microhabitat (Goebel 1890; Ruinen 1961; Winkler 1967, 1970; Pócs 1996; Sonnleitner et al. 2009). About one thousand species of epiphyllous bryophytes have been described. Apparently, they have certain morphological characters which allow them to colonize and survive in this ephemeral environment. Epiphylls have long been recognised as the phyllosphere of vascular plant communities (Ruinen 1961). Several studies have been conducted on morphological and life-history characters related to the survival of epiphylls and the correlation of microclimatic variables with the distribution of epiphyllous communities (Gradstein 1997; Gignac 2001; Wanek and Pörtl 2005; Frego 2007; Sonnleitner et al. 2009; Hylander et al. 2013; Malombe et al. 2016).

Sabah, located at the East of Malaysia, consists of several unique landscapes and regions of higher altitudes that offer promising biological sites for the study of epiphyllous liverworts. Much of this region has been declared either as state parks under the management of Sabah Parks or conservation areas under the management of Yayasan Sabah Group. For example, the Crocker Range, the longest range in Sabah extending from Kudat (northern tip of Borneo) to Sipitang (southern part of Sabah) (Suleiman et al. 2017), has the highest mountain peak in Southeast Asia (Mount Kinabalu, 4059 m a.s.l), together with other 16 peaks that exceed 1,000 m above sea level (Usui et al. 2006). Meanwhile, huge areas of unique landscapes (basin, valley, coast, canyon and river) that have been protected host a remarkable biological diversity with a staggering number of plant species.

A fair number of bryophyte studies have been published and reported from Sabah (e.g., Mizutani 1974; Inoue 1989; Yamada 1989; Piippo 1989; Frahm et al. 1990; Akiyama et al. 2001; Suleiman et al. 2006; Andi et al. 2015; Zhu et al. 2017). However, no specific study focused on epiphyllous liverwort communities has been conducted in tropical rainforests of Sabah and within Malaysia. Therefore, the present study is aimed to evaluate the species richness and beta diversity of epiphyllous assemblages from three selected localities in Sabah by performing a phytosociological survey and detailed statistical analysis.

Materials and methods

Study area

1) Ulu Senagang

Ulu Senagang is located in the western part of Sabah (Fig. 1), near the boundary of Tenom and Keningau districts. It is part of the Crocker Range Park (CRP) and located in the south eastern zone of the park. The CRP was shaped by the Crocker Range Formation where the lower part is of Paleocene to Middle Eocene age (Hutchison 2005). The most dominant parental soil types found in the Crocker Range are sandstone and mudstone (Dinor et al. 2007). The temperature on the lowlands of CRP is within 22–40 °C throughout the year. CRP has one of the highest precipitation areas in Sabah. However, the eastern part of the park, including Ulu Senagang, has a relatively low rainfall with less than 2,000 mm/year (Usui et al. 2006). The forest vegetation zone of Ulu Senagang is lowland rainforest and it is classified as hill dipterocarp forest. According to Majit et al. (2011), the forest type of this area is considered as a young secondary forest due to past disturbance from human activities and forest fires.

2) Mount Silam

Mount Silam is a small coastal mountain located at the south-eastern part of Sabah in Lahad Datu district (Fig. 1). Most of the mountain is made up of ultrabasic rock. Standing at only 884 m a.s.l., this mountain experiences frequent cloud cap formation which usually develops from the early afternoon until the end of the day. The forest above 770 m

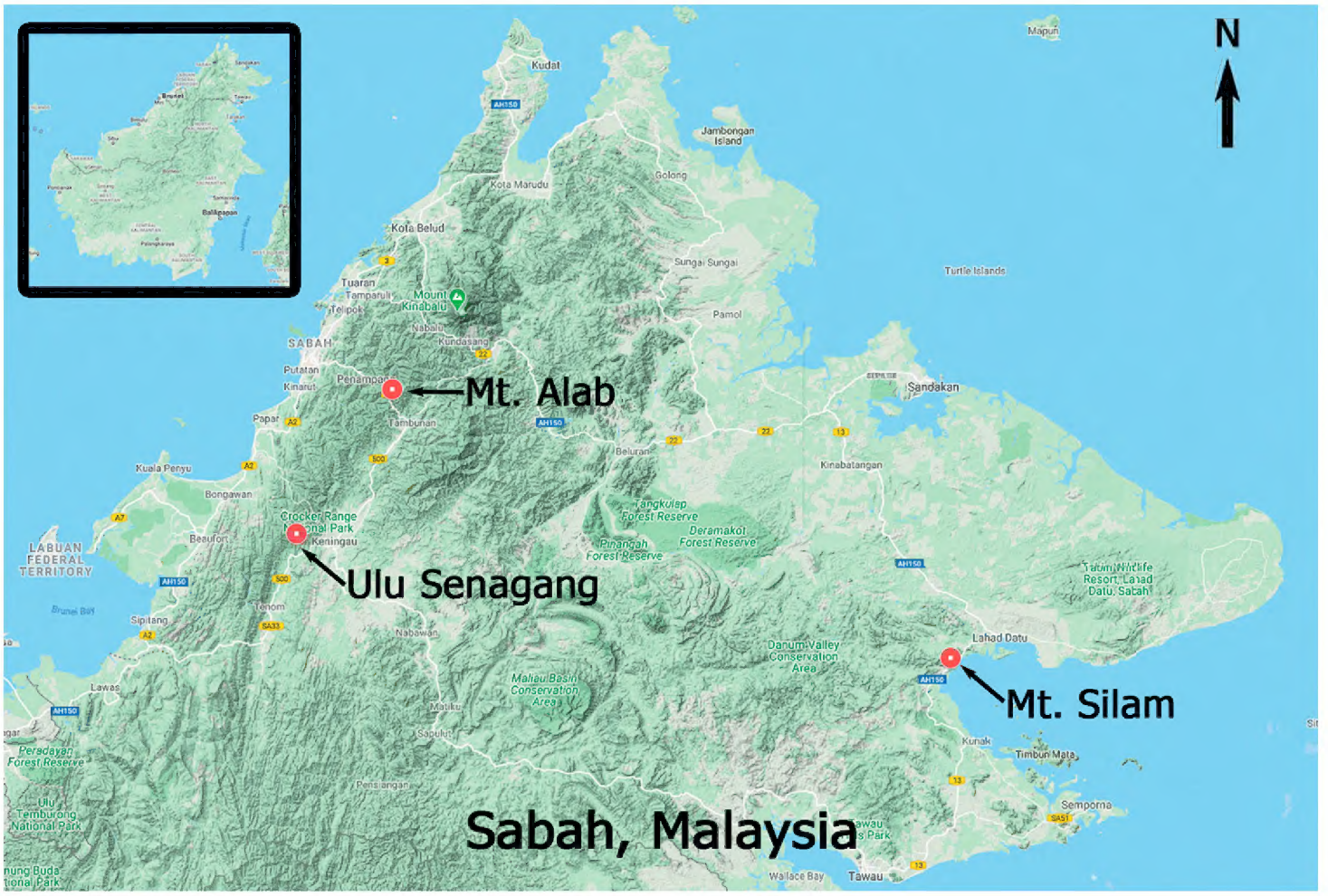

Figure 1. The three selected localities in the present study.

is stunted, showing a classic 'Massenerhebung effect', which is the compression of forest zones on a small mountain (Proctor et al. 1988). The altitudinal gradient of Mount Silam can be divided into four layers which are the lowland ultramafic forest (200–300 m), upland ultramafic forest (330–540 m), lower montane ultramafic forest (540–770 m) and the upper montane ultramafic forest (>770 m) (Sabah Forestry Department 2017). The lowland climate of Mount Silam is humid tropical with an average precipitation of 2,132 mm/year. The annual mean temperature is 27 °C and the mean monthly relative humidity is about 85%. However, the summit region receives higher rainfall of up to 2,700 mm/year and relative humidity of 90–91% (Bruijnzeel et al. 1993). The mean temperature of the summit region is 18.8–27.7 °C (Proctor et al. 1988).

3) Mount Alab

Mount Alab is located in the northern zone of the Crocker Range Park in Tambunan district. This area shares the same geological formation and soil types with Ulu Senagang. This mountain is the second highest peak of CRP with 1964 m a.s.l. The forest vegetation zone of this area is upper montane rainforest, called also "cloud- or "mossy-forest". It is classified as a primary forest and dominated by montane plants from the Fagaceae, Myrtaceae and Ericaceae. Mount Alab receives the highest rainfall in CRP with more than 4000 mm/year. The mean air temperature and relative humidity of this mountain are about 15 °C and 99%, respectively (Majuakim and Anthony 2016). The peak of Mount Alab is persistently covered with clouds from mid-day, resulting in high abundance of bryophytes.

Sampling and data analysis

During our present study in Malaysia, by the selection and guidance of the second author, we studied 23 rainforest habitats in Sabah. Of these we could take representative samples of the epiphyllous communities in 12 habitats at different altitudes. The routine followed the sampling protocol of Pócs (1978). For the present study, we selected three sites: Crocker Range Park, W of Keningau district at Ulu Senagang Substation (a lowland rainforest at 525–570 m elevation); Crocker Range Park, NNW of Tambunan district at Gunung Alab Substation (mossy elfin forest or cloud forest at 1900–1940 m elevation); and Mt. Silam, Sapagaya Forest Reserve of Lahad Datu district (lower montane rainforest at 600–740 m elevation). From the shrub layer of each site, 50 average sized leaves well-covered by epiphylls were collected randomly and prepared for further study. From a coenological point of view, each leaf was considered to be a different stand of the epiphyllous assemblage. The species composition on each leaf was identified, yielding a total of 98 species. That is, the present study is based on a 98 × 150 presence-absence data matrix, as given separately for the three study areas in Tables 2–4. In addition, the area of each leaf was also measured.

The epiphyllous liverwort assemblage data served as a basis for a detailed statistical survey. The relationship between the number of species and leaf area was graphically illustrated by a scatterplot, and standard correlation and regression analyses were conducted to evaluate its linear component. Centered (i.e. covariance-based) principal component analysis (Podani 2001) was used to generate a simultaneous ordination of species and leaves, the biplot. In addition, beta diversity and related structural phenomena were evaluated by the SDR simplex method developed by Podani and Schmera (2011).

Results and discussion

The localities of epiphyllous collections and phytosociological survey

Table 1 shows the enumeration of rainforest habitats visited during the period of 30 July to 17 August, 2018 in which epiphyllous liverworts were collected. In Tables 2–4, each column represents the epiphyll flora of one leaf. The leaf area in cm^2 and the number of species of each leaf are indicated. The X and + symbols mean presence only, while the black dots in Table 3 indicate the dominant species on each leaf. The species

Table 1. The three investigated habitats in the present study.

	Locality	Forest type	GPS coordinates	Elevation (m)
Table 2.	**1822.** Ulu Senagang Substation, Crocker Range Park, Keningau district	Lowland rainforest below waterfalls, with 50 m high canopy of Dipterocarpaceae	05°21.776'N, 116°01.713'E	525–570
Table 3.	**1811.** Mt. Silam, Sapagaya Forest Reserve, 22 km WSW of Lahad Datu district, from the telecommunication towers to the summit ridge of Mt. Silam	Lower montane rainforest with 15–20 m high canopy with *Shorea tenuiramulosa* and *Borneodendron enigmaticum*.	04°57'12"N, 118°9'39"E	600–740
Table 4.	**1823.** Mt. Alab Substation, Crocker Range Park, Tambunan district	Mossy cloud (elfin) forest, about 6 m high canopy of *Phyllocladus hypophyllus*, *Rhododendron*, *Dacrydium* and *Nepenthes* spp.	05°49.320'N, 116°20.499'E.	1900–1940

Table 2. The epiphyllous communities in Ulu Senagang, a lowland tropical rainforest at 525–570 m elevation.

Leaf surface area in cm²	130	44	120	150	38	145	115	46	17	70	120	30	42	96	45	240	130	12	230	14	44	13	85	41	70
Cover of epiphylls in % of leaf surface	5	25	70	2	20	10	40	4	15	30	18	7	12	18	40	9	5	55	8	40	50	65	8	18	20
Species number of each leaf	8	5	10	4	6	5	8	4	5	9	8	6	4	4	8	5	6	3	4	4	3	5	7	2	6
Leptolejeunea epiphylla (Mitt.) Steph.	.	.	X	X	X	X	X	.	X	.	X	.	.	X	X	.	.	.	X	X	X	.	X	.	X
Leptolejeunea maculata (Mitt.) Schiffn.	X	X	.	X	X	.	X	X	X	X	X	X	X	X	.	X	.	.	X	X	.	.	X	X	.
Cololejeunea planissima (Mitt.) Abeyw.	X	.	X	X	X	X	.	.	.	X	X	.	.	.	X	X	X	X	X	X	.	.	.	.	X
Cololejeunea gottschei (Steph.) Mizut.	X	.	.	.	X	.	.	.	X	X	.	X	X	.	.	X	X	X	.	X	.	.	X	.	X
Lejeunea sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	X	.	.	X	.	.	.	.
Drepanolejeunea tenera K.I.Goebel	.	.	X	.	.	.	X	X	.	.	X	X	.	X	.	X	.	.	.	.	.	.	X	.	X
Cheilolejeunea trapezia (Nees) R.M.Schust. & Kachroo	.	.	X	.	.	.	X	.	.	X	.	.	X	.	.	.	.	.	.	.	.	X	.	.	.
Cololejeunea lanciloba Steph.	.	X	.	.	.	.	.	.	X	.	.	.	.	.	.	.	X	.	X	.	.	.	X	.	.
Cololejeunea longifolia (Mitt.) Mizut.	.	.	.	.	.	.	.	X	.	X	X	.	.	X	.	.	.	.	.	.	.	.	.	.	.
Leptolejeunea vitrea (Nees) Schiffn.	X	.	X	.	.	X	X	X	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Microlejeunea punctiformis Taylor (Steph.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.
Cololejeunea hildebrandii (Austin) Steph.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.
Cololejeunea peponiformis Mizut.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.
Drepanolejeunea pentadactyla (Mont.) Steph.	.	.	.	.	.	X	.	.	X	X	.	X	X	.	.	.	.	.	.	.	.	.	.	.	.
Lejeunea sp.2	X	X	.	.	X	.	X	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.
Caudalejeunea reniloba (Gottsche) Steph.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	X	.	.	.	.	.	X	.	.
Cololejeunea tenella Benedix	.	X	.	.	X	.	X	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Colura acroloba (Steph.) Ast	.	.	X	X	.	.	X	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Frullania sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	X	.	.	.	.	.	.	.	.
Lopholejeunea subfusca (Nees) Schiffn.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	X	.	.	.
Cololejeunea acuminata Mizut.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cololejeunea raduliloba Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	X	X
Drepanolejeunea vesiculosa (Mitt.) Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	.	X	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.
Cheilolejeunea (*Cyrtolejeunea*?)	X	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Colura conica (Sande Lac.) K.I.Goebel	X	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Colura corynophora (Nees et al.) Trevis	.	.	.	.	.	.	.	.	.	.	X	.	.	.	X	.	.	.	.	.	.	.	.	.	.
Leptolejeuna ligulata Herzog	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.
Leptolejeunea tripuncta (Mitt.) Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X
Cheilolejeunea intertexta (Lindenb.) Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cheilolejeunea vittata (G.Hoffm.) R.M.Schust & Kachroo	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cololejeunea aff. *schmidtii* Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cololejeunea stylosa (Steph.) Mizut.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.
Colura superba (Mont.) Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.
Colura ornata K.I.Goebel	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.
Lejeunea flava (Sw.) Nees	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lopholejeunea nigricans (Lindenb.) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Microlejeunea filicuspis (Steph.) Heinrichs et al.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 2. (Continued)

Leaf surface area in cm²	23	70	120	50	66	63	36	90	27	42	98	56	240	66	44	39	44	100	28	38	17	20	28	100	75	B
Cover of epiphylls in % of leaf surface	**12**	**6**	**5**	**6**	**7**	**8**	**30**	**8**	**28**	**24**	**60**	**5**	**3**	**30**	**14**	**10**	**5**	**30**	**4**	**16**	**12**	**30**	**7**	**9**	**45**	**50**
Species number of each leaf	**5**	**5**	**6**	**4**	**4**	**4**	**6**	**8**	**1**	**3**	**3**	**4**	**5**	**3**	**9**	**9**	**10**	**5**	**4**	**3**	**7**	**3**	**5**	**5**	**4**	
Leptolejeunea epiphylla (Mitt.) Steph.	X	.	X	.	X	X	.	X	.	X	X	X	X	X	X	X	.	X	.	X	X	X	X	X	X	32
Leptolejeunea maculata (Mitt.) Schiffn.	X	X	X	.	X	X	.	X	.	X	.	.	X	.	X	X	X	.	.	.	X	.	X	X	X	32
Cololejeunea planissima (Mitt.) Abeyw.	.	X	X	.	.	.	.	.	.	.	.	.	.	.	.	X	.	X	X	X	X	.	.	X	.	22
Cololejeunea gottschei (Steph.) Mizut.	X	X	X	.	.	.	.	.	.	.	.	.	.	.	X	X	X	.	.	.	X	.	.	.	.	19
Lejeunea sp.	X	.	.	.	X	X	X	X	.	.	.	X	X	.	.	X	X	.	X	X	X	X	X	.	X	18
Drepanolejeunea tenera K.I.Goebel	.	.	.	X	.	.	.	X	.	.	.	.	.	.	X	.	X	X	.	.	X	.	X	.	.	16
Cheilolejeunea trapezia (Nees) R.M.Schust. & Kachroo	.	.	.	.	.	.	X	X	X	.	.	X	.	X	X	X	X	X	.	.	.	X	.	.	.	15
Cololejeunea lanciloba Steph.	X	.	X	X	.	.	.	.	.	.	.	X	X	.	.	.	X	.	.	.	.	.	.	.	.	11
Cololejeunea longifolia (Mitt.) Mizut.	.	.	.	X	.	X	.	.	.	.	.	.	.	X	X	.	.	.	X	.	X	.	X	.	.	11
Leptolejeunea vitrea (Nees) Schiffn.	.	.	.	.	.	.	.	.	.	X	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
Microlejeunea punctiformis Taylor (Steph.)	.	.	.	.	.	.	X	X	.	.	.	.	.	.	X	.	X	.	.	.	.	.	.	.	X	6
Cololejeunea hildebrandii (Austin) Steph.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	X	.	.	X	.	.	.	.	X	.	5
Cololejeunea peponiformis Mizut.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	X	X	.	.	.	.	.	.	.	.	5
Drepanolejeunea pentadactyla (Mont.) Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Lejeunea sp.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Caudalejeunea reniloba (Gottsche) Steph.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Cololejeunea tenella Benedix	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Colura acroloba (Steph.) Ast	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Frullania sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	X	.	.	.	.	.	.	.	4
Lopholejeunea subfusca (Nees) Schiffn.	.	X	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Cololejeunea acuminata Mizut.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	X	.	3
Cololejeunea raduliloba Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Drepanolejeunea vesiculosa (Mitt.) Steph.	.	.	.	.	.	.	X	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
Cheilolejeunea (*Cyrtolejeunea*?)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Colura conica (Sande Lac.) K.I.Goebel	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Colura corynophora (Nees et al.) Trevis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Leptolejeuna ligulata Herzog	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Leptolejeunea tripuncta (Mitt.) Steph.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Cheilolejeunea intertexta (Lindenb.) Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	1
Cheilolejeunea vittata (G.Hoffm.) R.M.Schust & Kachroo	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	1
Cololejeunea aff. *schmidtii* Steph.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cololejeunea stylosa (Steph.) Mizut.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Colura superba (Mont.) Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Colura ornata K.I.Goebel	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Lejeunea flava (Sw.) Nees	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Lopholejeunea nigricans (Lindenb.) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	1
Microlejeunea filicuspis (Steph.) Heinrichs et al.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	1

Table 3. The epiphyllous communities in Mt Silam, a lower montane rainforest at 600–740 m elevation.

Leaf surface area in cm²	33	100	50	63	100	62	42	94	68	25	25	65	100	57	48	26	25	72	130	65	110	52	85	19	21
Cover of epiphylls in % of leaf surface	60	85	35	65	18	16	30	28	30	15	18	38	28	80	35	40	18	8	30	48	12	30	65	45	2
Species number of each leaf	2	4	9	5	8	6	11	7	9	4	8	3	6	5	4	2	3	4	8	3	11	4	6	2	3
Drepanolejeunea tricornua Herzog	●	+	+	●	●	.	●	●	●	.	.	●	●	+	●	●	.	+	●	●	●	●	●	●	.
Drepanolejeunea pentadactyla (Mont.) Steph.	.	.	+	.	+	.	+	+	.	.	.	+	+	●	+	+	.	.	●	.	+	.	.	.	.
Leptolejeunea aff. *balansae* Steph.	.	.	+	+	+	●	+	.	+	.	.	.	+	.	+	.	.	+	+	.	+	.	.	+	+
Cheilolejeunea trapezia (Nees) R.M.Schust. & Kachroo	.	+	+	+	+	+	+	.	.	.	.	+	●	.	.	.	.	.	+	+	+	+	+	.	.
Leptolejeunea amphiophthalma Zwickel	.	.	+	.	+	.	.	.	.	.	.	.	+	+	.	.	+	.	+	.	+	.	.	.	.
Colura corynophora (Nees et al.) Trevis	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Cololejeunea mutabilis Benedix	.	.	.	.	.	.	+	+	.	+	+	.	.	.	.	.	.	+	.	.	+	+	+	.	.
Colura conica (Sande Lac.) K.I.Goebel	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.
Colura sp.	.	+	+	+	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Drepanolejeunea dactylophora (Nees et al.) Schiffn.	+	●	●	+	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cololejeunea equialbi Tixier	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	+	.	.	.	+	.	+	.	.
Cololejeunea metzgeriopsis (K.I.Goebel) Gradst. et al.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.
Metalejeunea cucullata (Reinw. et al.) Grolle	.	.	.	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Colura superba (Mont.) Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cololejeunea stylosa (Steph.) Mizut.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Colura cristata Ast	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	●	.	.	.	.	.	.	.	.
Microlejeunea lunulatiloba Horik.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Microlejeunea punctiformis (Taylor) Steph.	.	.	.	.	.	.	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tuyamaella serratistipa S.Hatt.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Cheilolejeunea parvidens B.M.Thiers	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	+	.	.
Lejeunea papilionacea Prantl.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Cheilolejeunea ventricosa (Schiffn.) Xiao L.He	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Cololejeunea papillosa (K.I.Goebel) Mizut.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+
Colura maxima Ast	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Frullania apiculata (Reinw. et al.) Dumort.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lejeunea exilis (Reinw. et al.) Grolle	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lejeunea micholitzii Grolle	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leptolejeunea aff. *punctata* Herzog	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Acromastigum bancanum (Sande Lac.) A.Evans	.	.	.	.	.	.	.	.	.	.	●	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cheilolejeunea ceylanica (Gottsche) R.M.Schust.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cheilolejeunea intertexta (Lindenb.) Steph.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cheilolejeunea meyeniana (Nees et al.) R.M.Schust. & Kachroo	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Cheilolejeunea occlusa (Herzog) T.Kodama & N.Kitag.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cheilolejeunea trifaria (Reinw. et al.) Mizut.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 3. (Continued)

Cheilolejeunea sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Cololejeunea haskarliana (Lehm. & Lindenb.) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Cololejrunea obliqua (Nees & Mont.) Schiffn.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Colura acroloba (Steph.) Ast	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	
Colura aff. *mosenii* Steph.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Diplasiolejeunea cavifolia Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	
Diplasiolejeunea sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Drepanolejeunea longicornua (Herzog) Mizut.	.	.	●	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Drepanolejeunea serricalyx Herzog	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	
Drepanolejeunea ternatensis (Gottsche) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Lejeunea cf. *tuberculosa* Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Lepidolejeunea bidentula (Steph.) R.M.Schust.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Leaf surface area in cm²	**90**	**52**	**150**	**150**	**55**	**160**	**106**	**120**	**136**	**130**	**45**	**65**	**42**	**110**	**8**	**41**	**16**	**36**	**19**	**155**	**72**	**20**	**15**	**120**	**120**	**50**	
Cover of epiphylls in % of leaf surface	**25**	**55**	**5**	**5**	**55**	**20**	**15**	**8**	**10**	**45**	**50**	**35**	**70**	**6**	**12**	**40**	**60**	**18**	**15**	**5**	**20**	**40**	**30**	**15**	**5**		
Species number of each leaf	**4**	**5**	**6**	**4**	**4**	**7**	**3**	**4**	**5**	**3**	**1**	**4**	**3**	**3**	**4**	**6**	**3**	**4**	**6**	**9**	**4**	**4**	**2**	**4**	**1**		
Drepanolejeunea tricornua Herzog	●	+	.	.	●	●	●	.	●	●	●	●	●	.	●	●	●	●	.	.	.	●	●	.	+	37	
Drepanolejeunea pentadactyla (Mont.) Steph.	+	●	●	.	●	+	●	+	+	.	.	+	+	.	.	+	+	+	.	.	.	+	+	.	.	26	
Leptolejeunea aff. *balansae* Steph.	.	.	.	●	+	.	+	+	+	.	.	.	.	●	.	+	+	+	.	●	●	+	.	●	.	26	
Cheilolejeunea trapezia (Nees) R.M.Schust. & Kachroo	+	.	+	.	+	.	.	.	+	+	.	+	.	.	.	+	.	.	.	+	.	.	.	.	.	21	
Leptolejeunea amphiophthalma Zwickel	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	10	
Colura corynophora (Nees et al.) Trevis	.	+	.	.	.	+	.	●	.	+	.	.	+	.	.	+	.	.	+	.	.	.	.	.	.	9	
Cololejeunea mutabilis Benedix	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	
Colura conica (Sande Lac.) K.I.Goebel	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	+	.	.	.	+	.	7	
Colura sp.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	
Drepanolejeunea dactylophora (Nees et al.) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	7	
Cololejeunea equialbi Tixier	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	
Cololejeunea metzgeriopsis (K.I.Goebel) Gradst. et al.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	6	
Metalejeunea cucullata (Reinw. et al.) Grolle	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	6	
Colura superba (Mont.) Steph.	.	.	.	+	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	5	
Cololejeunea stylosa (Steph.) Mizut.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	4	
Colura cristata Ast	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	4	
Microlejeunea lunulatiloba Horik.	.	.	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	4	
Microlejeunea punctiformis (Taylor) Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	
Tuyamaella serratistipa S.Hatt.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	4	
Cheilolejeunea parvidens B.M.Thiers	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	
Lejeunea papilionacea Prantl.	.	.	●	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	3	
Cheilolejeunea ventricosa (Schiffn.) Xiao L.He	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	
Cololejeunea papillosa (K.I.Goebel) Mizut.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	

Table 3. (Continued)

Colura maxima Ast	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	2
Frullania apiculata (Reinw. et al.) Dumort.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	2
Lejeunea exilis (Reinw. et al.) Grolle	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Lejeunea micholitzii Grolle	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	2
Leptolejeunea aff. *punctata* Herzog	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	2
Acromastigum bancanum (Sande Lac.) A.Evans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cheilolejeunea ceylanica (Gottsche) R.M.Schust.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cheilolejeunea intertexta (Lindenb.) Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cheilolejeunea meyeniana (Nees et al.) R.M.Schust. & Kachroo	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cheilolejeunea occlusa (Herzog) T.Kodama & N.Kitag.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cheilolejeunea trifaria (Reinw. et al.) Mizut.	.	.	•	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cheilolejeunea sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1
Cololejeunea haskarliana (Lehm. & Lindenb.) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	1
Cololejrunea obliqua (Nees & Mont.) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Colura acroloba (Steph.) Ast	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Colura aff. *mosenii* Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Diplasiolejeunea cavifolia Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Diplasiolejeunea sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1
Drepanolejeunea longicornua (Herzog) Mizut.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Drepanolejeunea serricalyx Herzog	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Drepanolejeunea ternatensis (Gottsche) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1
Lejeunea cf. *tuberculosa* Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1
Lepidolejeunea bidentula (Steph.) R.M.Schust.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1

Table 4. The epiphyllous communities in Mt. Alab, a mossy cloud (elfin) forest at 1900–1940 m elevation.

Leaf surface area in cm²	**100**	**75**	**72**	**100**	**60**	**60**	**70**	**35**	**80**	**63**	**36**	**100**	**35**	**16**	**67**	**22**	**27**	**50**	**15**	**60**	**36**	**207**	**41**	**26**	**120**
Cover of epiphylls in % of leaf surface	**30**	**12**	**30**	**28**	**15**	**40**	**70**	**40**	**20**	**25**	**30**	**8**	**30**	**45**	**8**	**15**	**18**	**14**	**55**	**30**	**30**	**25**	**65**	**65**	**2**
Species number of each leaf	**10**	**7**	**5**	**8**	**10**	**8**	**70**	**4**	**6**	**11**	**7**	**9**	**6**	**7**	**4**	**4**	**5**	**7**	**8**	**8**	**4**	**13**	**7**	**9**	**4**
Drepanolejeuna thwaitesiana (Mitt.) Steph.	X	X	.	.	X	X	X	X	.	X	X	X	X	.	X	.	X	X	X	.	.	X	X	.	.
Diplasiolejeunea jovet-astiae Grolle	X	X	.	X	.	X	.	.	X	X	.	X	.	X	.	.	X	.	X	.	.	X	.	.	.
Drepanolejeunea dactylophora (Nees et al.) Schiffn.	.	.	.	X	.	.	X	.	.	X	X	X	X	.	X	X	X	.	X	X	.	.	X	.	X
Cololejeunea peraffinis (Schiffn.) Schiffn.	.	X	.	.	X	X	X	.	.	X	X	.	X	X	.	X	.	X	X	X	.	X	X	X	X
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	.	X	X	.	X	.	X	X	X	.	.	.	.	.	.	.	.	X	.	X	.	.	.	.	X
Drepanolejeunea pentadactyla (Mont.) Steph.	X	.	X	X	.	.	X	X	.	.	X	X	.	.	.	.	.	.	X	.	X	X	.	.	.
Microlejeunea punctiformis (Taylor) Steph.	X	.	.	.	X	.	.	.	X	X	.	X	.	.	.	.	.	.	.	X	.	X	.	X	.
Drepanolejeunea tenera K.I.Goebel	.	.	.	.	X	.	.	.	X	.	X	.	.	.	.	.	X	.	.	X	.	.	.	X	.
Cololejeunea haskarliana (Lehm. & Lindenb.) Schiffn.	.	.	X	.	.	.	X	.	.	.	X	.	.	.	.	X	.	.	X	.	X	.	X	X	.
Drepanolejeunea vesiculosa (Mitt.) Steph.	X	.	.	X	.	X	.	.	.	.	.	X	X	X	.	.	.	.	X	.	.	.	.	.	.
Cololejeunea ensifera Tixier	.	X	.	.	.	.	.	.	.	X	.	.	X	.	.	X	.	.	.	.	.	.	X	.	X
Leptolejeunea subdentata Herzog	.	.	X	.	X	X	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Frullania ramuligera (Nees) Mont.	X	.	.	X	.	.	.	.	.	.	.	X	.	X	.	.	.	X	.	.	.	X	.	.	.
Cololejeunea dozyana (Sande Lac.) Schiffn.	.	.	.	X	.	X	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.
Cololejeunea macounii (Underw.) A.Evans	.	.	.	.	X	.	.	.	.	.	.	.	.	.	X	.	X	.	.	.	.	.	.	.	.
Cololejeunea stephanii Benedix	.	X	X	.	.	.	.	.	X	.	.	.	.	.	X	.	.	.	.	.	.	.	X	.	.
Cheilolejeunea trapezia (Nees et al.) R.M.Schust. & Kachroo	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	X	.	X	.
Colura tenuicornis (A.Evans) Steph.	.	.	.	X	X	.	.	X	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.
Lejeunea flava (Sw.) Nees	X	.	.	.	X	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.
Cololejeunea papillosa (K.I.Goebel) Mizut.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	X	.
Cololejeunea sphaerodonta Mizut.	.	.	.	.	.	.	X	.	.	.	X	.	.	.	.	.	.	.	X	.	X	X	.	.	.
Colura verdornii Herzog & Ast	.	X	.	.	X	X	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	X	.	.	.
Drepanolejeunea aff. *serricalyx* Herzog	.	.	.	.	.	.	.	.	.	.	.	X	X	.	.	.	.	.	.	X	.	.	X	.	.
Lejeunea sp.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	X	.
Leptolejeunea maculata (Mitt.) Schiffn.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.
Frullania sp.	X	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.
Drepanolejeunea fissicornua Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Microlejeunea constricta (Grolle) Grolle	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.
Radula tjibodensis K.I.Goebel	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.
Schiffneriolejeunea tumida (Nees) Gradst.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cheilolejeunea aff. *ventricosa* (Schiffn.) Xiao L.He	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.
Cheilolejeunea occlusa (Herzog) T.Kodama & N.Kitag.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.
Cheilolejeunea meyeniana (Nees et al.) R.M.Schust. & Kachroo	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.
Cololejeunea cf. *filicaulis* Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.

Table 4. (Continued)

Cololejeunea magnilobula (Horik.) S.Hatt.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Cololejeunea sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Colura sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Drepanolejeunea teysmannii Steph.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Drepanolejeunea ternatensis (Gottsche) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Lopholejeunea eulopha (Taylor) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	
Metalejeunea cucullata (Reinw. et al.) Grolle	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Myriocoleopsis minutissima (Sm.) R.L.Zhu et al.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Leaf surface area in cm²	**20**	**40**	**13**	**30**	**54**	**20**	**26**	**12**	**5**	**10**	**13**	**43**	**20**	**50**	**145**	**18**	**110**	**65**	**13**	**20**	**60**	**86**	**60**	**93**	**20**	**FR**
Cover of epiphylls in % of leaf surface	**20**	**65**	**60**	**16**	**2**	**20**	**19**	**25**	**60**	**5**	**50**	**10**	**25**	**45**	**8**	**25**	**8**	**14**	**40**	**15**	**9**	**12**	**12**	**9**	**60**	**A**
Species number of each leaf	**5**	**3**	**6**	**5**	**4**	**5**	**4**	**5**	**6**	**5**	**5**	**6**	**6**	**7**	**5**	**7**	**9**	**9**	**6**	**7**	**8**	**6**	**7**	**9**	**4**	**50**
Drepanolejeuna thwaitesiana (Mitt.) Steph.	X	X	X	X	X	X	.	X	.	X	.	X	.	X	X	X	X	.	.	.	X	.	X	X	.	32
Diplasiolejeunea jovet-astiae Grolle	X	.	X	X	.	X	X	.	X	X	X	.	.	.	.	X	X	X	X	X	X	.	X	X	.	26
Drepanolejeunea dactylophora (Nees et al.) Schiffn.	X	.	X	X	X	.	X	X	X	.	X	X	X	X	.	X	.	.	.	.	.	.	.	X	.	26
Cololejeunea peraffinis (Schiffn.) Schiffn.	.	.	.	.	.	.	.	X	.	.	.	.	X	X	.	.	X	.	.	.	.	.	X	X	X	22
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	X	.	X	.	.	X	.	.	X	.	.	.	.	.	X	X	X	X	.	.	X	X	.	X	.	21
Drepanolejeunea pentadactyla (Mont.) Steph.	.	X	.	.	.	.	.	.	.	X	.	.	.	X	.	.	.	X	X	.	.	X	X	X	.	18
Microlejeunea punctiformis (Taylor) Steph.	.	.	.	.	.	.	.	.	.	.	X	X	.	.	.	X	.	X	X	X	X	.	.	X	.	16
Drepanolejeunea tenera K.I.Goebel	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	X	X	X	X	X	X	.	.	.	X	13
Cololejeunea haskarliana (Lehm. & Lindenb.) Schiffn.	.	.	X	X	.	.	.	.	X	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	12
Drepanolejeunea vesiculosa (Mitt.) Steph.	.	.	.	.	.	.	.	.	.	.	X	X	.	.	.	.	.	X	X	.	.	.	.	X	.	12
Cololejeunea ensifera Tixier	.	.	.	.	.	.	.	.	X	.	X	.	X	.	.	.	.	X	.	X	.	.	.	.	.	11
Leptolejeunea subdentata Herzog	.	.	.	.	.	X	.	.	.	.	.	.	.	.	X	X	.	.	.	.	X	X	X	.	.	10
Frullania ramuligera (Nees) Mont.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	X	.	.	X	.	.	.	.	.	9
Cololejeunea dozyana (Sande Lac.) Schiffn.	.	.	X	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	X	.	X	8
Cololejeunea macounii (Underw.) A.Evans	.	X	.	X	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	X	X	.	.	8
Cololejeunea stephanii Benedix	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	X	.	.	.	8
Cheilolejeunea trapezia (Nees et al.) R.M.Schust. & Kachroo	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	X	.	.	.	X	.	.	X	.	7
Colura tenuicornis (A.Evans) Steph.	X	.	.	.	.	X	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
Lejeunea flava (Sw.) Nees	.	.	.	.	X	.	.	.	.	.	.	.	X	.	.	.	.	.	X	.	.	.	.	.	.	6
Cololejeunea papillosa (K.I.Goebel) Mizut.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	X	.	.	.	.	.	.	.	.	.	.	5
Cololejeunea sphaerodonta Mizut.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Colura verdornii Herzog & Ast	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Drepanolejeunea aff. *serricalyx* Herzog	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	5
Lejeunea sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	X	.	.	.	.	.	.	.	5
Leptolejeunea maculata (Mitt.) Schiffn.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	4

Table 4. (Continued)

Frullania sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	3
Drepanolejeunea fissicornua Steph.	.	.	.	.	.	.	.	.	X	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	2
Microlejeunea constricta (Grolle) Grolle	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Radula tjibodensis K.I.Goebel	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Schiffneriolejeunea tumida (Nees) Gradst.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	2
Cheilolejeunea aff. *ventricosa* (Schiffn.) Xiao L.He	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cheilolejeunea occlusa (Herzog) T.Kodama & N.Kitag.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cheilolejeunea meyeniana (Nees et al.) R.M.Schust. & Kachroo	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cololejeunea cf. *filicaulis* Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cololejeunea magnilobula (Horik.) S.Hatt.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Cololejeunea sp.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Colura sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	1
Drepanolejeunea teysmannii Steph.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Drepanolejeunea ternatensis (Gottsche) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	1
Lopholejeunea eulopha (Taylor) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Metalejeunea cucullata (Reinw. et al.) Grolle	.	.	.	.	.	.	.	.	.	.	.	.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Myriocoleopsis minutissima (Sm.) R.L.Zhu et al.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1

Table 5. The comparison of the epiphyllous assemblages of three localities in terms of the number of occurrences of constituting liverwort species.

Locality	Ulu Senagang	Mt. Silam	Mt. Alab	Total
Leptolejeunea maculata (Mitt.) Schiffn.	32	26	4	62
Drepanolejeunea pentadactyla (Mont.) Steph.	5	24	18	47
Cheilolejeunea trapezia (Nees et al.) R.M.Schust. & Kachroo	15	21	7	43
Microlejeunea punctiformis (Taylor) Steph.	6	4	16	26
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	3	1	21	25
Leptolejeunea epiphylla (Mitt.) Steph.	32	.	.	32
Cololejeunea planissima (Mitt.) Abeyw.	22	.	.	22
Cololejeunea gottschei (Steph.) Mizut.	19	.	.	19
Cololejeunea lanciloba Steph.	11	.	.	11
Cololejeunea longifolia (Mitt.) Mizut.	11	.	.	11
Leptolejeunea vitrea (Nees) Schiffn.	8	.	.	8
Cololejeunea hildebrandii (Austin) Steph.	5	.	.	5
Cololejeunea peponiformis Mizut.	5	.	.	5
Colura corynophora (Nees et al.) Trevis	2	9	.	11
Colura conica (Sande Lac.) K.I.Goebel	2	6	.	9
Lejeunea sp. 2	5	1	.	6
Colura acroloba (Steph.) Ast	4	1	.	5
Colura superba (Mont.) Steph.	1	4	.	5
Drepanolejeunea tricornua Herzog	.	37	.	37
Leptolejeunea amphiophthalma Zwickel	.	11	.	11
Cololejeunea mutabilis Benedix	.	8	.	8
Colura sp.	.	7	.	7
Cololejeunea equialbi Tixier	.	6	.	6
Cololejeunea metzgeriopsis (K.I.Goebel) Gradst. et al.	.	6	.	6
Colura superba (Mont.) Steph.	.	5	.	5
Drepanolejeunea tenera K.I.Goebel	16	.	13	29
Lejeunea sp.	18	.	5	23
Drepanolejeunea vesiculosa (Mitt.) Steph.	3	.	12	15
Frullania sp.	4	.	3	7
Lejeunea flava (Sw.) Nees	1	.	6	7
Drepanolejeunea dactylophora (Nees et al.) Schiffn.	.	7	26	35
Cololejeunea haskarliana (Lehm. & Lindenb.) Schiffn.	.	1	12	13
Metalejeunea cucullata (Reinw. et al.) Grolle	.	6	1	7
Cololejeunea papillosa (K.I.Goebel) Mizut.	.	2	5	7
Cheilolejeunea occlusa (Herzog) T.Kodama & N.Kitag.	.	1	1	2
Drepanolejeuna thwaitesiana (Mitt.) Steph.	.	.	32	32
Diplasiolejeunea jovet-astiae Grolle	.	.	26	26
Cololejeunea peraffinis (Schiffn.) Schiffn.	.	.	22	22
Cololejeunea ensifera Tixier	.	.	11	11
Leptolejeunea subdentata Herzog	.	.	10	10
Frullania ramuligera (Nees) Mont.	.	.	9	9
Cololejeunea dozyana (Sande Lac.) Schiffn.	.	.	8	8
Cololejeunea macounii (Underw.) A.Evans	.	.	8	8
Cololejeunea stephanii Benedix	.	.	8	8
Colura tenuicornis (A.Evans) Steph.	.	.	7	7
Cololejeunea sphaerodonta Mizut.	.	.	5	5
Colura verdoornii Herzog & Ast	.	.	5	5
Drepanolejeunea aff. *serricalyx* Herzog	.	.	5	5

are arranged according to their frequency in the analysed communities. Table 5 shows the comparison of the three assemblages, their similarities and differences, in which species with at least 10% occurrence in Tables 2–4 are included only. Those with frequency less than 5 out of 50 are omitted.

Species/leaf area relationships and beta diversity analyses

The number of species vs leaf area relationships are shown by the scatter plot in Fig. 2. Although the variance of the number of species per leaf is fairly high, there is a definite increase of species number over area. Since the number of points is large, and therefore the degrees of freedom is also large (n = 148), the resulting Pearson correlation, $r = 0.22$ with a probability point of $p = 0.007$, is a highly significant result. The regression equation is $N = 0.01A + 4.93$ in which N is the estimate of species number at leaf area A expressed in cm^2.

The entire data set was evaluated by centered principal component analysis. The first two ordination axes explain 14% and 10% of the total variance. Although these percentages may appear low at first sight, the biplot diagram for axes 1–2 (Fig. 3) is well-interpretable. The leaves from the three sites form separate clusters, oriented away from the origin in three directions. The three sites do not separate completely, the species-poor leaves are positioned around the centroid. The length and position of arrows indicate species that are most responsible for the differences between the three sites. It is seen that site number 1 in Fig. 3, i.e. Mt. Alab has a fairly large number of species

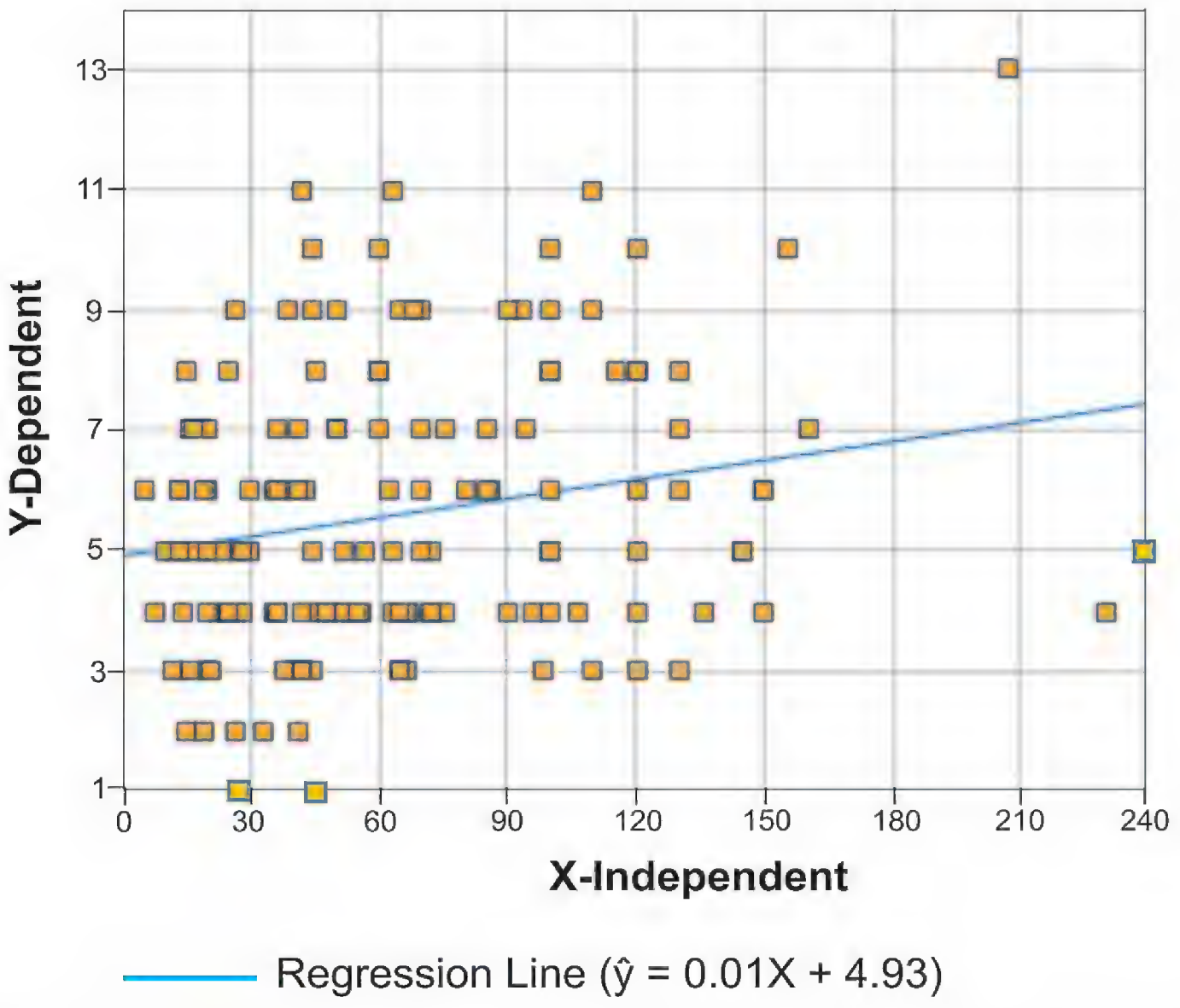

Figure 2. Leaf area (in cm^2, x axis) – number of epiphyll liverwort species (y axis) relationship based on 150 leaves collected in three rainforest sites in Sabah.

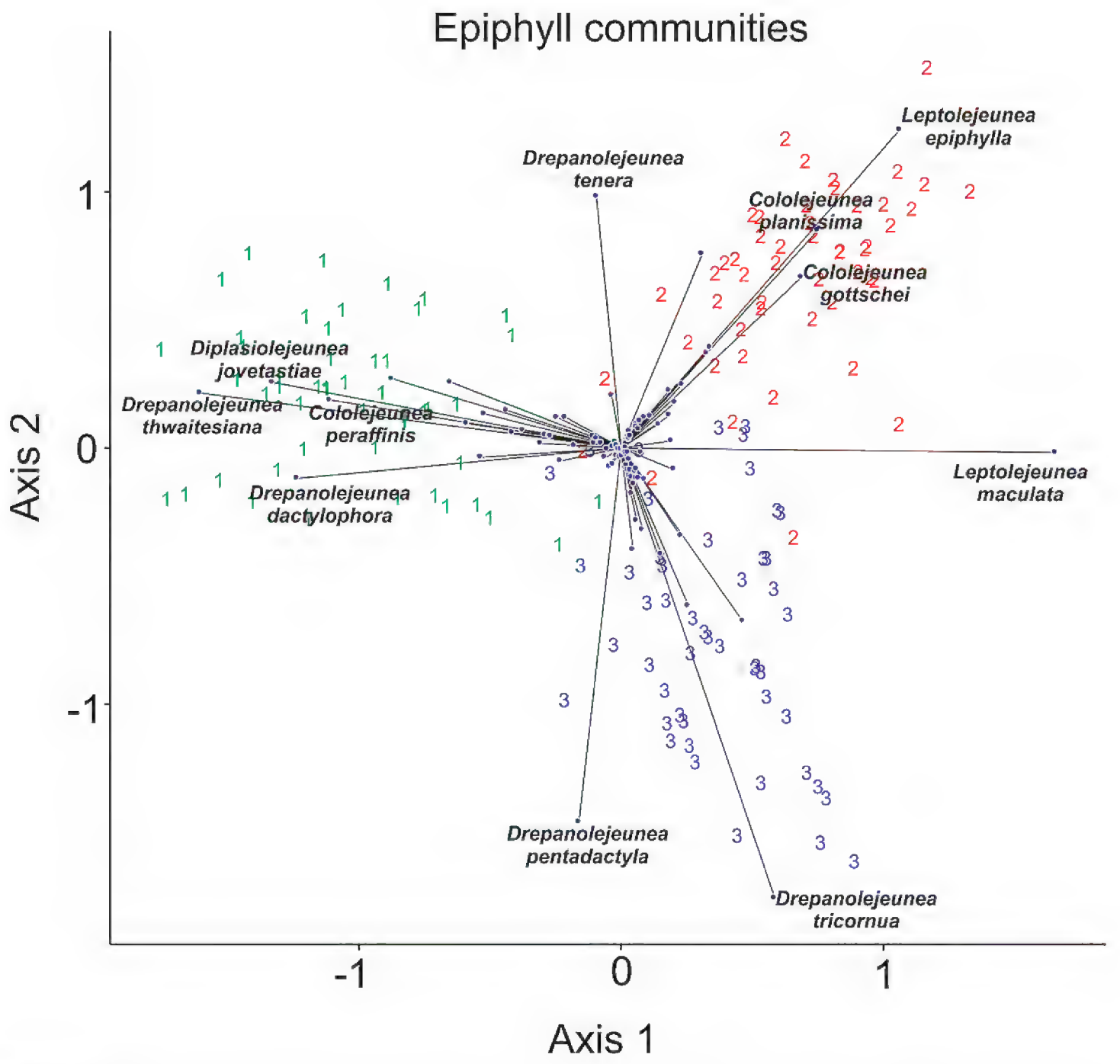

Figure 3. The Principal Components ordination biplot of the three groups of epiphyllous assemblages, each containing 50 leaves. Numbers identify forest sites **1** mossy cloud (elfin) forest, Mt. Alab (Table 4) **2** lowland rainforest, Ulu Senagang (Table 2) **3** lower montane rainforest, Mt. Silam (Table 3).

that typically occur there, such as *Diplasiolejeunea jovet-astiae* Grolle, *Drepanolejeunea thwaitesiana* (Mitt.) Steph., *D. dactylophora* (Nees, Lindenb. & Gottsche) Schiffn. and *Cololejeunea peraffinis* (Schiffn.) Schiffn. Site 2 in Ulu Senagang is mostly characterized by the presence of *Leptolejeunea epiphylla* (Mitt.) Steph., *Cololejeunea gottschei* (Steph.) Mizut. and *C. planissima* (Mitt.) Abeyw., whereas *Drepanolejeunea tenera* K.I.Goebel occurs in both sites. In site 3 (Mt. Silam, a lower montane rainforest near to the sea, exposed to rain carrying winds), *Drepanolejeunea pentadactyla* (Mont.) Steph. and *D. tricornua* Herzog appear most typical. Most species are positioned near the origin, showing that they are either relatively rare as *Cololejeunea macounii* (Underw.) A.Evans or *Colura superba* (Mont.) Steph. or common to all the three sites like *Leptolejeunea maculata* (Mitt.) Schiffn.

The SDR simplex plot and associated percentages obtained for the entire study area (three sites taken together) demonstrate that there is an extremely high beta di-

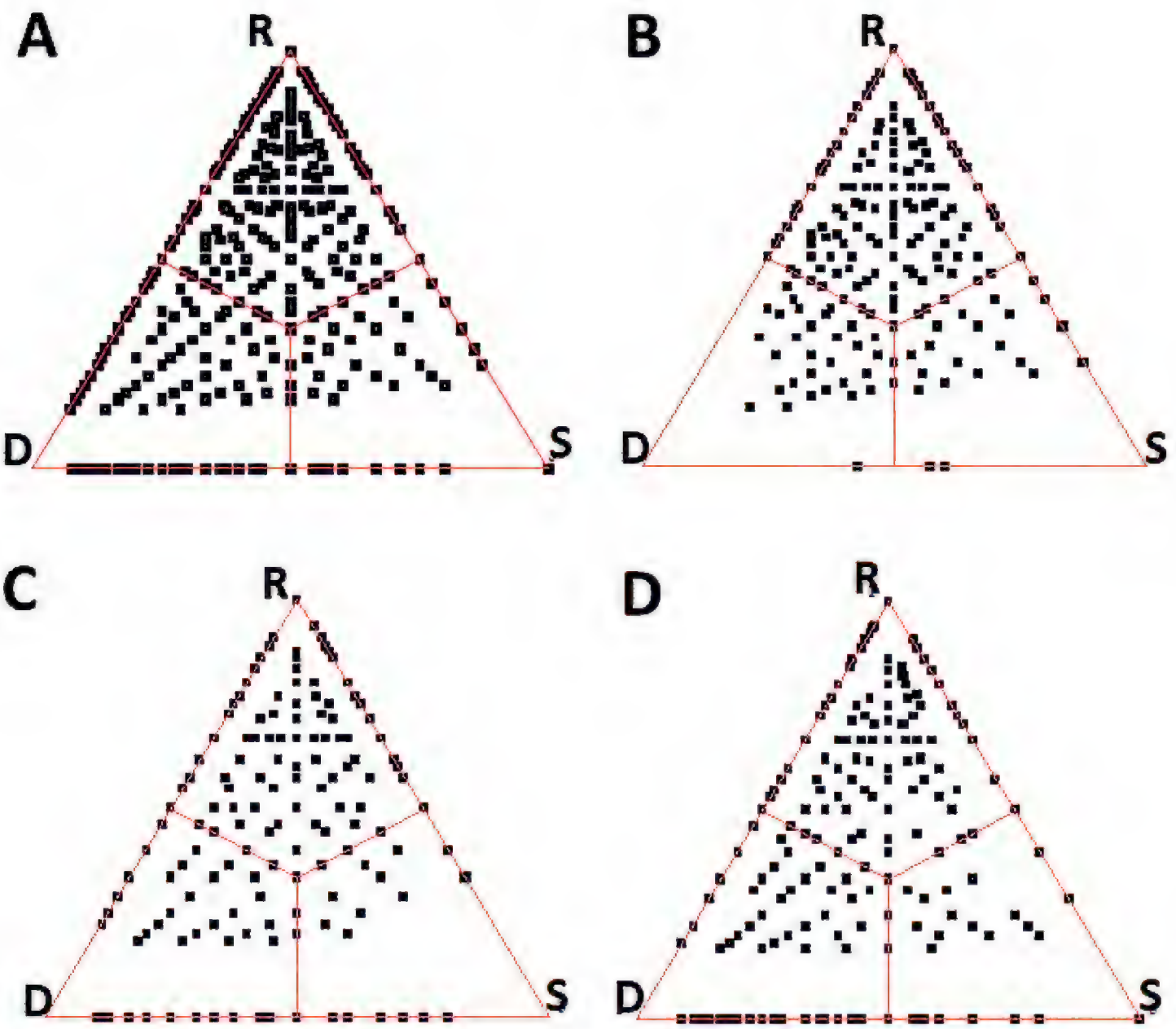

Figure 4. Ternary (or simplex) plot for the epiphyllous liverwort assemblages based on presence-absence data for three rainforest sites in Sabah **A** all sites taken together **B** mossy cloud (elfin) forest, Mt. Alab **C** lowland rainforest, Ulu Senagang **D** lower montane rainforest, Mt. Silam.

versity (91%) of epiphyllous assemblages in the study sites, leaving only a 9% share by similarity (Fig. 4A). Beta diversity is dominated by turnover (species replacement, R = 66%) while richness difference (D) is 25%. Its graphical manifestation is that most of the points (each representing a pair of leaves) lie within or near the upper third of the triangle (R – replacement). The anti-nestedness fraction within beta diversity, corresponding to points lying on the left edge of the triangle, is 11% – this is caused by pairs of leaves that do not have a single species in common. Nevertheless, quite many points lie on the bottom side, demonstrating that nestedness is also characteristic of the epiphyllous bryophyte assemblages – the species occurring in certain leaves are subsets of the species assemblage of other leaves (D + S – Anti-nestedness fraction = 22.5%). The three simplex diagrams obtained for the three forests (Fig. 4B–D) show that the very high overall beta diversity is not merely the result of between-site differences; their beta diversity is 81%, 80% and 80.5%, leaving 19–20% for the similarity component. That is, the liverwort assemblages on the leaves of rainforest trees are extremely diverse. A major difference between the sites is in the partitioning of beta in which species

replacement is the highest in the cloud forest, i.e. in Mt. Alab (60%), and the lowest in the lowland montane forest in Mt. Silam (50.5%). This explains why nestedness is much less conspicuous in the cloud forest than elsewhere in which only a few points fall onto the bottom side of the plot.

Conclusion

The overall conclusion is that the major component of pattern formation in epiphyllous liverwort assemblages from Sabah is species replacement (50–60% for individual forests, 66% for combined data), while richness difference is less pronounced (20–25%). This is in contrast to the results of a study performed on similar assemblages in southern Thailand (Pócs and Podani 2015), where differences in species number were much more influential than species replacement (50% versus 37%). In any case, beta diversity – the sum of richness difference and species replacement – is extremely high in both studies, leaving only 10–20% similarity in the species composition of leaf surfaces. The ecological explanation is that the assemblage of a given leaf is likely to be formed by a random choice from the liverwort species pool of the forest, species follow one another haphazardly as allowed by the size of the leaf. In Sabah, the three forests selected for the present study were floristically very different, forming three clusters in the PCA ordination plane with a couple of characteristic species in each. Their separation was not sharp at all, species-poor leaves were arranged around the centroid regardless of their origin, and three sites were overlapping. Extended studies involving more forests from Malaysia, as well as from other areas in south-eastern Asia, may give further insight into the structure of this special type of plant communities.

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